

Seed germination in sedges: a short review

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Abstract: Five patterns of seed germination in the sedges of the genus *Carex* are presented, based on the literature data and the results of the authors' own research. They include the pattern of *C. acutiformis*, *C. arenaria*, *C. remota*, *C. flava* and *C. communis*. These patterns were constructed on the basis of seed specific requirements for development, such as stratification, temperature, dormancy and time of germination. Majority of sedges follow the pattern of *C. acutiformis* or *C. remota*. In both cases, stratification and either high or low temperature are essential for seed germination. Seeds that start to germinate early (*C. remota* pattern) are characterized by the absence of the distinct peaks of germination, as opposed to the *C. acutiformis* pattern with the germination peak in March. Our long-term investigations, conducted on the group of individuals in controlled conditions, revealed significant differences in seed size and the ability of seeds to germinate depending on the age of mother plants. We postulate that mother plant age is a new factor that should be considered in the construction of seed germination patterns.

Key words: *Carex*, light, temperature, utricle

1. Introduction

Studies on seed morphology and germination have long attracted scientific interest. This interest arises from the potential application of these studies to solving problems of such disciplines as ecology, genetics, taxonomy and evolutionary biology. Investigations into seed germination and dormancy allow to explain life strategy of a species and its distribution and spreading in different environments (e.g. Cain *et al.* 2000; Simons & Johnston 2000; Phartyal *et al.* 2009). For example, Aponte *et al.* (2010) described seed development and germination ecology of invasive species *Prunus serotina* in order to know what controls the timing of germination under natural and/or synanthropic conditions. Their studies therefore enhance the understanding of invasion success of *P. serotina*.

Seed shape and size and the amount of endosperm affect seedling germination and survival and, in consequence, determine the reproductive success of an individual. Moreover, investigations into seed morphology, length of dormancy period and seed dispersal are particularly useful in taxonomic research (e.g. Yamada *et al.* 2001; Berg 2009), especially for the following taxons: Ericaceae (Fagúndez *et al.* 2010; Lu *et al.* 2010), Bora-

ginaceae (Özcan 2008) or Gentianaceae (Davitashvili & Karrer 2010). Studies of soil seed banks and germination conditions allow to predict the dynamics of plant communities and the direction of succession (e.g. Kobayashi & Kamitani 2000; Kudoh & Whigham 2001; Morris *et al.* 2002; Egawa *et al.* 2009; Ne'eman *et al.* 2009).

Despite such widespread interest in seeds and their germination, there is not much known about the process of germination in sedges of the genus *Carex*, which is one of the largest and most widespread genera of vascular plants. Species of this genus occur on every continent (except Antarctic) and in almost every habitat (Egorova 1999). The aim of this article is to review available data on factors affecting sedge seed germination and to make an attempt to synthesize these data in the form of seed germination patterns characteristic for this group of plants.

2. Taxonomy and distribution of the genus *Carex*

In 1753, Carl Linnaeus in his work, *Species Plantarum*, distinguished 29 species of sedges and placed them in a newly created genus *Carex*. Since then, botanists have described over 2000 species belonging to this genus

and distinguished over 70 sections grouped into various subgenera. In terms of the number of species, *Carex* is one of the largest genera within the family *Cyperaceae* (Reznicek 1990). At present, there are many competing hypotheses that explain phylogenetic relationships among species of sedges and, in consequence, many competing classification systems. This is particularly evident at the subgenus level. Kükenthal (1909), Reznicek (1990) and Egorova (1999) have based the classification of sedges at the subgenus level on the inflorescence structure. These authors, irrespective of the number of distinguished subgenera, agree that: (1) unisexual spikes are typical of the subgenera *Kreczetoviczia* and *Carex*, (2) bisexual female-male spikes are typical of the subgenus *Indocarex*, (3) bisexual spikes, both male-female and female-male, are characteristic of the subgenus *Vignea*, (4) apical bisexual spikes, male-female and male and female, are typical of the subgenus *Primocarex* (*Psyllophora*).

Species of the genus *Carex* are widely distributed over the world but are mostly found in the temperate zones of both hemispheres, with the main centers of distribution in North America, Central and Northern Europe and Eastern Asia (Reznicek 1990). They can be found in highly diverse environments, ranging from cold mountainous areas (eg. *Carex nivalis* – 5475 m a.s.l.) and dry, open savannas (eg. *Carex swanii*) to tropical regions (eg. *Carex rodesiaca* and *Carex zuluensis*). They also occur in wet meadows, broadleaf and conifer forests and in Arctic tundra (Egorova 1999).

3. Seeds of sedges – morphology, dispersal and use in taxonomy

The fruit of sedges is monospermous, indehiscent, with a hard pericarp enclosed in the utricle. There are two or three stigmas of different length in different species. Stigmas are usually longer in forest taxa. Embryo length is $\frac{1}{4}$ of seed length and endosperm is fairly abundant (Egorova 1999). Polyembryony has been observed in some species of *Carex*, i.e., seeds with two embryos may be formed, e.g. in *C. pendula* and *C. arenaria*. Seeds of sedges are relatively small – about 0.8 mg in weight (Leck & Schütz 2005). Differences in seed size among sedges that occur in different habitats have been found. In many species, populations of a given species produce smaller seeds in dry habitats than in wet habitats (Leck & Schütz 2005).

The main way of sedge diaspores dispersal is barochory, although seeds may be also transported by the wind (e.g. *C. physodes*), water (e.g. *C. rostrata*, *C. riparia*) or animals: epizoochorously (*C. pseudocyperus*, *C. bohémica*) or endozoochorously (*C. baccans*). Some forest species are myrmecochores (*C. digitata*, *C. ornitopoda*), while a small number of taxa are anthro-

chores. Frequently, from two to four different types of seed dispersal can be observed in a given species (Egorova 1999; Leck & Schütz 2005).

The following traits of sedge seeds are used in the genus taxonomy: (1) shape of a cross section through a utricle, (2) length of the base of a utricle (in some species it is absent), (3) shape of a beak, (4) edge of a sack, (5) wall layout, (6) presence or absence of hairs, (7) the number and length of veins and (8) size, shape and colour of a utricle (Egorova 1999).

4. Factors controlling germination

The most important factors that affect initiation and the course of germination are temperature and light. Moreover, our studies on sedge seed germination have shown a high importance of life history traits (Żukowski *et al.* 2005; Lembicz *et al.* 2010). Our experiment under controlled conditions of a garden allowed to observe the effect of mother plant age on the development of seeds and seedlings of *Carex secalina*. This sedge is a monoecious perennial plant with a tussock habit. It propagates exclusively from seeds (Fig. 1). We found that mean seed mass varied with plant age but the pattern of variation is population-specific, with only one population showing reduction in seed mass with mother plant age. Similarly, germination frequency changed with mother plant age differently in different populations, while relationship between the age of a mother plant and the length of emerged seedlings did not differ between the populations.

Because sedges grow in almost every habitat and on almost every continent, differences and similarities in requirements for germination among different species may have significant consequences for maintaining species diversity. These requirements are also vital to the implementation of proper tactics of species restoration, particularly in the case of endangered plants. In Poland, 22 species of sedges are threatened with extinction, listed in the Polish Red Data Book of Plants (Każmierczakowa & Zarzycki 2001), and there is very little known about the conditions of their germination.

4.1. Temperature

Temperature regulates the time of germination. Most of sedges requires rather high temperatures (10-30°C) (e.g. Schütz 2002; Brändel & Schütz 2005; Kettenring & Galatowitsch 2007), however, in some species, germination can be initiated at the temperature below 10°C (e.g. *Carex remota*). Most probably, this phenomenon can be connected with the type of habitat. Sedges that grow in forests require lower temperatures than sedges of open habitats. The optimum temperature for seed growth (measured as a final percentage of germination) before stratification is about 20-25°C, although, in some

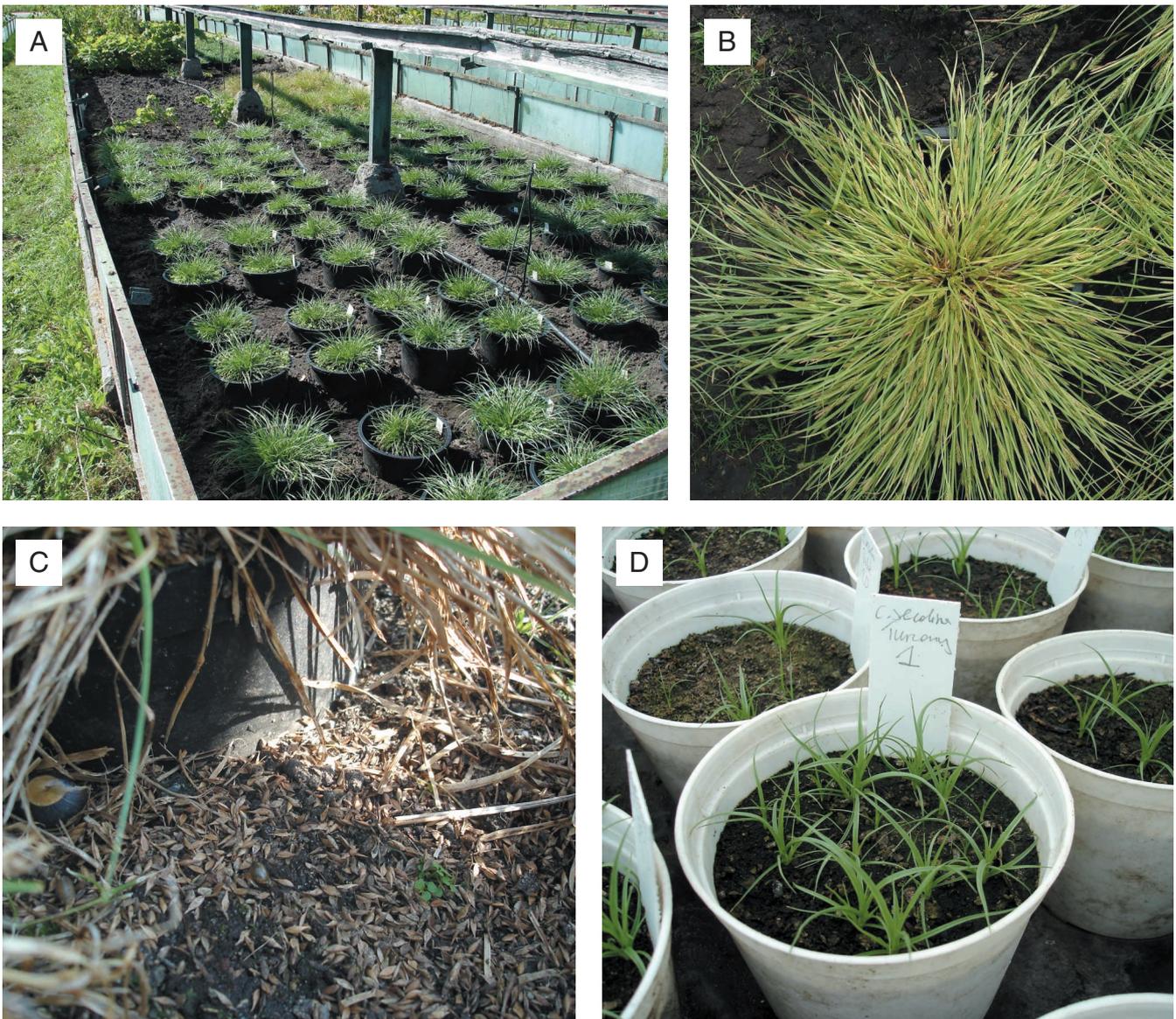


Fig. 1. Collection of the sedge *Carex secalina* in uniform garden conditions (Adam Mickiewicz University Botanical Garden in Poznań) Explanations: 100 plants were used in experiment that showed effect of mother plant age on the development of seeds and seedlings. A – collection of mother plants in the first year of life, B – an individual in the second year of life when it enters reproductive phase, C – *C. secalina* seeds scattered on the garden soil at the end of growing season, D – seedlings before removal from soil in order to estimate their size (photograph by A. Bogdanowicz)

species it fluctuates around 10°C (*C. sylvatica*) (Schütz 2000).

Overall, three types of responses to temperature have been found in the species of the genus *Carex*: (1) seeds are capable of germination at higher temperatures and after the break of secondary dormancy they still require high temperatures (species of the temperate climate), (2) seeds initially germinate at higher temperatures but after the break of secondary dormancy they require lower temperatures, (3) seeds germinate at medium temperatures but in the course of time they can also germinate at lower and higher temperatures (Schütz 2000).

The consequence of sedge adaptations to a wide range of environments is their sensitivity to diurnal fluctuations in temperature, i.e. many species does not ger-

minate under constant temperature conditions but under temperature fluctuations. Usually, an increase in a percentage of germinating seeds is more strongly correlated with soil temperature fluctuations than with constant temperatures. Similar differences were observed in seeds after stratification. However, the response to temperature fluctuations may differ between species. Some sedges germinate well under constant temperatures and under low fluctuations (species of dry grasslands, like *C. ericetorum* and *C. caryophylla*, and of wet habitats, e.g., *C. elongata* and *C. capillaris*), while others germinate poorly or do not germinate at all under constant temperatures. The response to temperature fluctuations does not reflect environmental conditions because the reaction of species of the genus *Carex* to temperature changes is quite uniform. Sedges of dry areas are in

general equally sensitive to an increase in temperature fluctuations as species of wet habitats (Schütz 2000).

4.2. Light

The sensitivity of seeds to light and temperature fluctuations may be subject to seasonal variation. Very often, some part of seeds within a population remains dormant in the dark, which is reflected in the higher percentage of germination in the light than in the dark. However, higher fluctuations of temperature may compensate light requirements in sedges of open habitats (e.g. *C. flava*, *C. elata*) that germinate equally well in the light as in the dark, at 22/12°C. Similar reactions may be caused by stratification. In many species of sedges, in certain stages of the dormancy cycle, often in early spring, when the daily fluctuations of temperature occur, a high percentage of germination in the dark has been observed (Schütz 2000). The response of sedge seeds to light differs between the species. Most species require longer periods of light to initiate germination, however, *C. elongata* and *C. curta* do not respond to the length of light exposure, while *C. ebenea* requires 15 days of continuous light at the minimum to initiate germination (Schütz 2000). Kettering *et al.* (2006) found different light response in eight species of sedges exposed to various lengths of daylight: for example *C. brevior* required <15 min to initiate germination, while *C. comosa*, *C. hystericina*, *C. granularis* and *C. vulpinoidea* >8h.

Seeds of sedges respond to far red light. Leaf litter is permeable to only a small amount of red light of c. 670 nm in wavelength but to a very large amount of far red light of c. 720 nm. The sensitivity to this factor allows seeds to avoid germination, even when temperature and humidity conditions are advantageous. Thanks to this, the probability of failure in seedling development due to the lack of light is reduced. Schütz (1998) found that some proportion of seeds of *C. extensa* and *C. arenaria* did not germinate under leaf litter but germinated under the thinned leaf layer in the following year. Seeds of all studied species germinated very quickly after moving them from a shady place to daylight. In six species of sedges of wet habitats, only limited germination was observed during exposure to far red light at 22/12°C, while the percentage of germination ranged from 0,4% in *C. panicea* to 30,8% in *C. davalliana* and was sometimes lower than in the dark (Schütz 2000). However, Ketterin *et al.* (2006) observed that an effect of daylight on germination may be substituted by red light in the eight examined species of sedges.

5. Dormancy cycles

Seasonal cycles of dormancy represent an adaptive strategy of plants of the temperate climate to varying

environmental conditions related to the change of seasons (Baskin & Baskin 1998). Some species avoid germination in summer and autumn, because seedlings may be exposed to a higher death risk due to high temperatures, lower availability of light and an increased probability of summer drought. In winter, the development of seedlings is restricted by the length of a vegetative period and a high risk of freezing. Seeds that germinate in spring remain dormant over winter, while in summer, they avoid germination due to the induction of secondary dormancy in response to high temperatures. Individuals, which did not germinate in spring, fall into dormancy in late spring or early summer (Schütz 1998).

Similar cycles of dormancy have been observed in sedges (e.g. Schütz 1997a; 1998; 2002). Seed dormancy is broken in autumn or in winter and towards the end of spring or in the early summer they fall into deep or relative dormancy. The dormancy induction depends on temperature. A high percentage of sedge seed germination was observed in early summer, at the temperatures of 10-12°C, while a low percentage was recorded at the end of summer, when temperature was 5-10°C higher. This indicates that seeds that are capable of germination usually induce dormancy in early summer, while in late autumn they can re-germinate (Schütz 1997b; 1998). Species of wet habitats, e.g. *C. stricta* and *C. comosa*, require higher temperatures to induce secondary dormancy, although similar relation was observed in some sedges growing on dry dunes (for example *C. arenaria*). It is difficult to unambiguously resolve, whether temperature related changes in dormancy are a 'phylogenetic constraint' or a consequence of environmental conditions (Schütz 2000).

It is possible that dormancy cycles can be induced by many other factors, because, e.g., seeds are capable of germination in the fluctuating temperature conditions (22/10°C) and they do not germinate in constant temperatures. An additional factor that controls seasonal dormancy is availability of water. A higher level of dormancy was observed in flooded seeds of *C. comosa* than in non-flooded seeds, in late summer and in autumn. Such behaviour may result from a low oxygen content in flooded soil (Baskin *et al.* 1996).

6. Seed longevity and soil bank

Seeds of *Carex* are long-lived (Schütz 1997a, 1998, 2002), as indicated by, among others, a small loss of seeds during germination and 'burial experiments'. In addition, seeds are often present in a soil bank, even when no mature plants are observed in the area. It has been found that the buried seeds of *C. flava* and *C. viridula* retain their viability for over six years, while in five other species (*C. scoparia*, *C. viridula*, *C. flava*, *C. elongata*, *C. curta*, and *C. pseudocyperus*), seeds were

viable for less than 5 years. Some studies have shown that sedge seeds are capable of germination for up to 130 years (see review Schütz 2000). It has also been demonstrated that seed viability is connected with storage conditions in the laboratory or in the soil (Leck & Schütz 2005). Even storage in cold conditions may reduce seed viability for up to 95% (Budelsky & Galatowitsch 1999). There are also other factors that may influence seed longevity, such as photoperiod, biotic factors, local inhibitors of germination, burial depth and soil characteristics (Baskin & Baskin 1998). In the genus *Carex*, these factors have not been thoroughly investigated so far. The differentiation in seed viability and their germinability may also result from genetic differences between populations or maternal effects during seed development. The study by Lembicz *et al.* (2010) has shown the connection between germination rate and age of a mother plant in *C. secalina*.

Majority of sedge species are able to form long-lived seed banks, because they fall in either relative or deep dormancy, require light for germination, show a low percentage of germination under constant temperature and under low daily fluctuations of temperature and induce secondary dormancy in summer. A long-lived seed bank, frequently buried at a large depth (>10 cm), secures survival of a population for up to 2-7 decades, as long as viable seeds are present in the soil. In right conditions, often, after removing the top layer of soil, an extinct species can be revived (Schütz 2000). The

study on 20 seed banks in the temperate European forest ecosystems revealed that seeds of sedges may be present in a seed bank, despite the absence of plants in vegetation (Schütz 2000).

Some species of sedges may form short-term seed banks or do not form them at all. The study by Leck & Schütz (2005) on seed banks in different habitats showed that, e.g., *C. acutiformis* does not form a seed bank, which results from habitat conditions. This species grows in tidal freshwater marsh sites, thus, its growth and dispersal is by rhizomes.

7. Patterns of germination

During the vegetation season, seeds of sedges behave similarly like seeds of other species. Usually we can observe two patterns. Few seeds may start to germinate and in the following season, the percentage of seedlings gradually decreases (like in *Stelaria media* and *S. nemorum*). The other pattern involves species that exhibit a high germination rate in the first year and in the next two years, the rate of germination is constant (like *Juncus effusus*, *Lapsana communis*) (Janowska-Błaszczuk 2000). Such behaviour may be connected with the seasonal cycles of dormancy, i.e., seeds avoid germination in adverse summer or winter conditions. Stratification is an essential factor for the development of the majority of *Carex* species, similarly like for many other plants of the temperate climate. Due to

Table 1. Patterns of seed germination in the sedges of the genus *Carex* constructed on the basis of seed specific requirements for development, such as stratification, temperature, dormancy and time of germination. These patterns are based on the literature data

Pattern	Germination requirements
<i>C. acutiformis</i>	Stratification High temperatures Temperature amplitude (22/10°C) Germination peak in March
<i>C. arenaria</i>	Stratification High temperatures but not as high as in <i>C. acutiformis</i> Constant temperatures Weaker dormancy than in <i>C. acutiformis</i> Germination peak in March
<i>C. remota</i>	Stratification Low temperatures Constant and varied temperatures Stable percentage of summer germination, no peaks Very early spring germination
<i>C. flava</i>	Stratification High temperatures Temperature amplitudes (22/10°C), in the light and in the dark Deep dormancy Germination peak in summer
<i>C. communis</i>	Absence of stratification High temperatures Weak dormancy Germination peak in June Myrmecochory

this mechanism, seeds can survive over winter and, after breaking dormancy, germinate in summer. In the temperate climate, the optimal temperature for sedge growth is about 10-30°C, similarly like for other plants of this climatic zone. Contrary to other taxa, high constant temperature (>25°C) does not substitute daily temperature fluctuations as a factor that speeds up germination.

Although patterns of sedge germination are quite similar, we distinguished five types of sedge germination patterns based on the specific requirements for seed development. Selected patterns are based on literature data and characterize specific germination requirements of a given species (for detailed information see articles cited earlier). These requirements include: (1) stratification, (2) temperature, (3) dormancy and (4) time of germination (Table 1). In four out of five patterns, seeds need stratification for germination (except the *C. communis* pattern) but in the first pattern of *Carex acutiformis* seeds also need high temperatures but with amplitude of temperatures (22/10°C). Germination peak is observed in March. Similarly, in the *C. arenaria* pattern, seeds require high temperatures but not as high as in *C. acutiformis*. Temperature should be constant during germination. Dormancy is weaker than in *C. acutiformis* but germination peak is also observed in March. In the *C. remota* pattern, seeds apart from stratification need low constant or varied temperatures. There are no peaks of germination. There is the stable rate of summer germination but seeds may germinate very early in spring. In the case of the *C. flava* pattern, seeds need high temperatures, temperature amplitudes (22/10°C) and deep

dormancy. Germination peak is observed in summer. Seeds of the *C. comunnis* pattern do not need stratification but need high temperatures. Dormancy is weak and germination peak is observed in June. Seeds are dispersed by ants.

8. Conclusions

In this article we presented available data on factors affecting sedge seed germination. We distinguished five types of sedge germination patterns based on the specific requirements for seed development. Effect of abiotic factors (such as temperature and light) on seed germination is well known but little attention has been paid to natural conditions affecting seed germination. A new methodological approach is required to fully understand conditions controlling germination of this group. Especially in the light of new studies that highlighted importance of life history traits of mother plants (Lembicz *et al.* 2010). Moreover, there is little known about the growth conditions of seeds of species occurring in the nutrient-poor and wet habitats of tropical and subtropical regions (Schütz 2000). This often makes difficult the comparison of germination requirements between the genus *Carex* and other closely related taxa, and, furthermore, the preparation of strategies of revegetation and protection of rare and threatened species and the maintenance of biodiversity.

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